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Wojnowicia graminis (McAlp.) Sacc. and D. Sacc. in relation to Foot Rot of Wheat in Australia

By

W. V. LUDBROOK, B.Agr.Sc., Ph.D.

MELBOURNE, 1936

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FOREWORD.

Wheat is subject to several well-known groups of diseases such as rusts, smuts, and root rots. The last-named group has recently been estimated to be the cause of a reduction in yield of 4 per cent. in one year in New South Wales. Such a loss is not always easily observable in the field, and yet it occurs in most seasons; it is thus the duty of pathologists to ascertain every fact which may lead to a reduction of the losses.

The problem of foot rot of wheat is admittedly one of extreme complexity, because several organisms may be involved as causes alone or in association, and each may be affected by soil, climatic, and other factors. The methods which are successful in the control of other wheat diseases do not give control of foot rot. It is becoming increasingly apparent that to make any headway it is necessary to advance our fundamental knowledge of the life of the microscopic organisms inhabiting the soil, including a determination of which are the fungi causing foot rot. One essential is to evaluate the relative importance of the several species of fungi which are frequently found in association with diseased tissues. That has been the object of the work reported in this Bulletin.

Wojnowicia graminis is widely distributed in Australia and other wheat-growing lands, and it is frequently found on the diseased basal parts of plants obviously suffering from foot rot. It was found in over half of the wheat fields inspected by officers of the Division of Plant Industry during an extensive survey in 1932, and accordingly was subjected to study. The results indicate that this organism is of little importance as a direct cause of foot rot in cereals, although it is still possible that it may have some significance in the general balance among the organisms inhabiting the soil of our wheat fields.

B. T. DICKSON,
Chief, Division of Plant Industry.

Canberra, F.C.T.,
August, 1936.

C.11005.—2

SUMMARY.

1. *Wojnowicia graminis* is widely distributed in the wheat-growing areas of Australia, and is frequently found on wheat plants suffering from foot rot.*

2. Cultural studies of the organism failed to reveal any important physiological differences between 85 isolates. Pycnidia were seldom produced in culture except on oat agar. The optimum and maximum temperatures for growth of the fungus on potato saccharose agar were 22°C. and 32°C. respectively; the minimum was below 5°C. The optimum pH was about 7.5.

3. Of four foot rot organisms tested under similar conditions, *W. graminis* had the least effect on wheat plants. It produced superficial brown to black discolouration on the basal parts of plants grown in infested soil, without any apparent ill effect on their growth as compared with that of controls.

4. The pathogenicity of *W. graminis* on wheat was practically unaltered by several variations in the treatment of inoculated plants, although some of the variations were designed to favour attack by even a weak parasite. No difference in pathogenicity was found between 50 representative isolates of the organism.

5. Concurrent infection with bunt or flag smut did not increase the susceptibility of wheat to attack by *W. graminis*.

6. The presence of *W. graminis* in the soil had no significant effect upon the susceptibility of wheat to attack by flag smut, bunt, or *Fusarium culmorum*.

7. *W. graminis* was isolated from 12 species of grasses and cereals, other than wheat, grown in pots of artificially infested soil. When the plants were grown in the field on artificially infested soil, attempted isolations from 4 of these species gave negative results.

8. Tests of 100 wheat varieties showed that they did not differ appreciably in their susceptibility to attack by *W. graminis*.

9. *W. graminis* was isolated from a number of apparently normal wheat plants at 4 stages of growth in the field, on soil infested with the organism. At 2 stages of growth, platings were also made from foot-rotted plants taken from the same crop. The percentage of plants from which *W. graminis* was isolated was higher in the former case than in the latter. *Fusarium culmorum* was isolated from a number of apparently healthy mature plants grown under similar conditions.

10. The yield of wheat was not reduced by *W. graminis* in any experiment. In several experiments, wheat yielded more heavily when grown in soil mixed with *W. graminis* inoculum than when grown in soil to which sterilized inoculum was added. Control plants grown in soil without inoculum yielded less than either of the above.

11. Under the conditions of these experiments, *W. graminis* is only very slightly, if at all, pathogenic on wheat. It may be somewhat more pathogenic on certain other hosts, e.g., barley grass (*Hordeum murinum*). No evidence has been obtained that it is of economic importance in Australia.

* The term "foot rot" is used throughout this paper to include the conditions known as root rot and white-heads.

Wojnowicia graminis (McAlp.) Sacc. and D. Sacc. in Relation to Foot Rot of Wheat in Australia.

1. Introduction.

Wojnowicia graminis (McAlp.) Sacc. and D. Sacc. was first described by McAlpine (15) in Victoria, under the name *Hendersonia graminis*. It was subsequently discussed, generally rather briefly, by investigators in France, Germany, Holland, North America, and Australia. Although the organism was frequently found in association with wheat showing foot rot symptoms in these countries, most workers were of the opinion that it was of minor, if any, importance as a pathogen (3, 6, 7, 8, 9, 10, 11, 12, 21, 22, 23, and 25). In the United States, it was first recorded by McKinney and Johnson (17). Guyot (14) and McKinney (16) reported experiments in which the organism appeared to exhibit some degree of pathogenicity on wheat. The literature was adequately reviewed in a recent paper by Sprague (22) who described the symptoms produced by the organism, discussed its taxonomy, and made a thorough investigation of its pathogenicity in the States of Oregon and Washington, United States of America. He found that it was very weakly pathogenic on a number of cereals and grasses and was of little or no economic importance.

The frequent association of *W. graminis* with foot rot of wheat in Australia (4, 15, 18, 19, also section 3 of this paper) suggested that it might be of some importance as a pathogen in this country. As far as the writer is aware, the only evidence in favour of this supposition was the frequent occurrence of the mycelium and pycnidia of the organism on the basal parts of diseased plants and its repeated isolation therefrom. In order to obtain experimental evidence as to the economic importance of *W. graminis,* the investigation of its pathogenicity under Australian conditions was assigned to the writer in 1932. The work reported in this paper was carried out at Canberra during the period 1933-1936.

2. Materials and Methods.

Most of the cultures used were isolated from material collected by the writer's colleagues on surveys made in Victoria and southern New South Wales, as mentioned in section 3. The writer also obtained representative cultures from workers in France, the United States of America, and South Australia.

Unless otherwise stated, the organism was grown for soil infestation on a mixture of equal parts by volume of barley and oats.* As the pathogenicity of the fungus was reputedly weak, large amounts of inoculum were used in most experiments (e.g., 50 to 70 gm. per six-inch pot). To allow for the possible manurial effect of the inoculum, an equal quantity, autoclaved at 15 lb. pressure for one hour just before

* Prepared by autoclaving the grain in excess of water for 30 minutes at 15 lb. pressure, draining off the water, placing the cooked grain as loosely as possible in plugged flasks, and again autoclaving for 30 minutes at 15 lb. pressure.

use, was added to some of the control pots. Others received neither sterilized* nor unsterilized inoculum. In some of the later pot experiments, a suspension of conidia washed from oat agar cultures was used as inoculum instead of the above. For large-scale field experiments, the fungus grown on barley-oats mixture was added to flats of freshly-sterilized sandy loam at the rate of 1 kilogram to 15 kilograms of soil, about three weeks before the inoculum was needed. The mixture was kept moist and protected from gross contamination until required. It was sprinkled at the rate of 2 kgm. (wet weight) per rod row, in the furrows in which the seed was to be sown. This was equivalent to an oven-dry weight of about 1,600 gm. per rod row.

The pot experiments were made during the period in which wheat is ordinarily grown in the district, and the plants were kept outside the greenhouse, except during the seedling and late ripening stages. Five plants were grown to maturity in each six-inch pot. The seed was not surface-sterilized, as preliminary experiments showed that this procedure was of no advantage. The inoculum was usually mixed with the top 2 inches of soil in each pot.

3. The Frequency of Occurrence of *W. graminis* in South-Eastern Australia.

The data in Table 1† are taken from the results of extensive surveys of wheat-growing areas in Victoria and southern New South Wales, made in order to study foot rot in the field and to determine approximately the relative frequency of occurrence of the principal foot rot organisms. Representative areas were traversed while the crop was in ear, and numerous specimens of diseased plants were collected from each field in which foot rot was found. This material was brought to the laboratory for microscopic examination and plating.‡ The areas covered by the two surveys were substantially the same, but no attempt was made in the second survey to re-visit the identical fields inspected previously.

In 1932, *W. graminis* and *Fusarium culmorum* each were found more than three times as often as either of the other two organisms most commonly associated with foot rot; in 1934, the proportion of fields yielding *W. graminis* fell from 56 per cent. (1932) to 12 per cent. One reason for this difference might be that the 1932 collections were made from crops approaching maturity, whereas those of 1934 were from crops many of which were in the flowering stage. Owing to differences in the ease with which the organisms may be isolated, the percentages given in Table 1 cannot be assumed to represent exactly the relative frequencies of their occurrence in the field.

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*Note that "sterilized inoculum" means barley-oats mixture overgrown with *W. graminis* and then autoclaved to kill the fungus. In no case did the writer use barley-oats mixture alone.

† Compiled from hitherto unpublished records kindly made available by the writer's colleagues, Dr. H. R. Angell and Mr. W. L. Geach, who made the surveys mentioned and under whose supervision the isolations were made.

‡ The method adopted for plating was as follows:—Stem-bases showing lesions or discolouration were washed and cut into pieces about ½ cm. long; these were surface-sterilized for 1½ minutes in 70 per cent. alcohol, rinsed in sterile water, and plated on potato saccharose or potato dextrose agar. A drop of 5 per cent. lactic acid was placed on each piece to impede bacterial growth.

TABLE 1.—RELATIVE FREQUENCIES WITH WHICH THE PRINCIPAL ORGANISMS ASSOCIATED WITH FOOT ROT OF WHEAT WERE ISOLATED FROM, OR DETERMINED IN, MATERIAL COLLECTED IN SOUTH-EASTERN AUSTRALIA DURING 1932 AND 1934.

Investigator.	Year.	Total Number of Wheat Fields Inspected Showing Foot Rot, or from which Foot Rot Organisms were Obtained.	Percentage of Fields in which the following Organisms were found.			
			Wojnowicia graminis.	*Fusarium culmorum.*	*Ophiobolus graminis.*	*Helminthosporium sativum.*
H. R. Angell	1932	153	56	56	17	14
W. L. Geach	1934	202	12	52	13	39

4. Studies of the Organism in Pure Culture.

(i) The occurrence of strains differing in appearance of thallus.

Eighty-five isolations of *W. graminis* from foot-rotted wheat plants were plated on potato saccharose agar; tentative classes were formed on the basis of thallus characters, and several representatives of each class were re-plated in two separate series to determine whether the differences persisted. Three classes could be regularly differentiated, one including the majority of isolates, and two containing isolates which consistently differed from those of the other groups more than from other individuals of the same group. Several single-spore cultures were made from each of four representative isolates; the cultures from each isolate were uniform and were similar to their parent culture. Representatives of each of the different classes of isolates were included in comparative tests of pathogenicity and temperature relationships, but no consistent variation in physiologic characters was found between members of the different groups. Sprague (22) also reported slight differences between strains of *W. graminis.*

(ii) Formation of pycnidia.

In the writer's experiments, pycnidia were seldom produced on potato saccharose or potato dextrose agars. The organism was grown on fourteen solid media, none of which favoured fruiting except oat agar.* On this medium, pycnidia and acervuli appeared more often than on any other medium tried, and sometimes in abundance. Foëx and Rosella (8) stated that pycnidia were produced on both oat and carrot agars, but more abundantly on the former. Some of the writer's cultures appeared to fruit more readily than others, but the fruiting tendency of a given isolate varied from time to time. Occasionally, one or more from a uniform lot of potato saccharose agar plates produced a number of more or less abortive pycnidia as the medium dried out. A few mature pycnidia were observed in tubes of cooked rice, and of potato saccharose agar, after several months' storage at

* Prepared by heating 100 gm. of rolled oats in 500 ml. of water at 60° to 70°C. for one hour, filtering through muslin, adding the filtrate to 500 ml. of water in which 17 gm. of agar was already dissolved, making up to 1,000 ml., tubing, and autoclaving for 30 minutes at 10 lb. pressure.

about 5°C. They were found in small numbers in the field on affected stubble in late summer, autumn, and winter. A few developed on wheat seedlings grown under aseptic conditions in glass tubes on Brenchley's agar (see section 5) inoculated with the organism. When sterilized soil was mixed with barley-oats inoculum and kept moist and cool (15° to 20°C.), large numbers of pycnidia sometimes appeared within a couple of weeks on the hulls of the grain projecting above soil level. Attempts to reproduce this phenomenon in flasks under aseptic conditions were not successful. Sprague (22) stated that spores were formed on sterile wheat heads, wheat kernels, and corn meal, in addition to the above-mentioned substances.

(iii) Size and appearance of pycnidia and conidia.

The measurements made by the writer are summarized in Table 2, and are compared with those of Broadfoot (3), Foëx and Rosella (8), McAlpine (15), Sprague (22), and Van de Laar (23). Distinct differences, both in size and appearance, were found by the writer between conida from different media, those formed on potato saccharose agar at 3° to 5°C. having a more marked olivaceous tinge, as well as being somewhat shorter and wider, than those from other sources. The differences between the measurements given by other authors might perhaps be partly accounted for by similar variations.

(iv) pH relations.

These were investigated by growing the fungus on potato saccharose agar adjusted to various pH values by adding hydrochloric acid or sodium hydroxide. Two separate experiments were made, in each of which eight lots of agar of different pH values were prepared, and five plates poured from each lot. Each plate was inoculated with a disc 5 mm. in diameter cut from near the edge of a young thallus of *W. graminis*. The diameters of the thalli were measured after 14 days' growth in diffused light at 16° to 20°C. The results showed that the organism did not grow on potato saccharose agar at or below pH 3.8. At pH 4.2, growth was slow, and the thalli were very abnormal in appearance, being of a reddish-orange colour with irregular edges. The growth increased and became more normal in appearance as the pH increased, up to an optimum in the region of pH 7.5. Moderate growth took place at pH 9.4, which was that of the most alkaline medium used. Yellowish tints predominated in the colonies grown on very acid media, and dark grey-green to greenish-black in those grown on nearly neutral or alkaline media. Determinations made at the end of the experiments indicated that the fungus tended to change the pH of both acid and alkaline media towards neutrality. Guyot (14) stated that acid media were strongly detrimental to the germination of conidia, which was stimulated by slight alkalinity.

(v) Temperature relations.

The organisms was grown on potato saccharose agar plates at a pH of about 6.3, inoculated with discs 5 mm. in diameter cut from near the edges of young thalli on the same medium. Twelve isolates were included in the tests, but no significant differences were found between their temperature relations. Three separate experiments were made. The optimum temperature for growth was about 22°C., and the maximum 33°. Slow growth took place at 5°, the lowest temperature employed. The fungus grew vigorously between 15° and 25°.

TABLE 2.—MEASUREMENTS (IN MICRONS) OF PYCNIDIA AND PYCNOSPORES OF *Wojnowicia graminis*, AND NUMBER OF SEPTA IN PYCNOSPORES.

Author	Nature and Source of Material.	Number of Measurements.	Length.			Breadth.			Number of Septa.		
			Average.	Minimum.	Maximum.	Average.	Minimum.	Maximum.	Average.	Minimum.	Maximum.
McAlpine	Pycnidia from field-grown wheat plants	..	360	..	..	240	..	..	..	..	..
Writer	„ „ „ „	25	345	247	432	290	185	432	..	..	..
Broadfoot ..	Pycnospores from a field-grown wheat plant	100	36·0	26·3	43·8	3·9	2·5	5·6	6·8	3	8
Foëx and Rosella ..	Pycnospores	..	..	30	36	..	3·5	5	..	..	..
McAlpine	Pycnospores from field-grown wheat plants	..	..	32	38	..	4	5	7	..	..
Sprague	„ „ „ „	50	..	29	36	..	4·6	5·7	..	..	..
„	„ „ „ „	50	37·9	31	46	4·9	4·2	7·2	..	..	..
„	Pycnospores from oat-barley grain culture	50	..	26·4	39·6	..	3·2	5·4	..	..	..
Van de Laar ..	Pycnospores	..	29·58	..	..	3·47	..	..	..	5	7
Writer	Pycnospores from field-grown wheat plants	25	37·0	28·8	43·2	4·2	2·9	6·5	6·4	3	7
„	Pycnospores from a potato saccharose agar culture	25	34·1	25·9	43·2	4·6	3·6	5·8	6·6	3	7
„	Pycnospores from a culture on cooked rice	75	31·9	25·0	38·7	3·7	3·1	4·4	6·4	3	7

5. Pathogenicity Tests.

(i) Comparison of the pathogenicity of *W. graminis* with that of other foot rot organisms.

Parallel inoculation experiments were made with *W. graminis* and the other organisms most commonly associated with foot rot of wheat in Australia, viz., *Ophiobolus graminis, Fusarium culmorum,* and *Helminthosporium sativum.* Wheat plants inoculated with these organisms separately were grown (*a*) under aseptic conditions on Brenchley's (2) solution of pH 6.2 solidified with 3 per cent. of agar, or on sterilized soil, in large glass tubes plugged with cotton wool; (*b*) in 300 ml. glass beakers of sterilized sand, watered with Brenchley's solution; (*c*) in six-inch pots of sterilized soil.

Under all the conditions tried, *W. graminis* was decidedly the least pathogenic of the four organisms. It readily produced superficial buff to dark-brown or greenish-black discoloured areas on the roots, mesocotyls,* stems, and leaf sheaths near the ground level, and was easily re-isolated from such areas. In spite of this, the growth of plants inoculated with *W. graminis* was never adversely affected by this organism.

Field experiments specially designed to compare the pathogenicity of *W. graminis* with that of the other foot rot organisms were not made, but four plots each of about four square chains, each inoculated with one of the organisms for the purpose of varietal resistance trials, were under the writer's observation for the past three seasons. The plots were situated at Duntroon, F.C.T., and were on moderately heavy silty loam, varying in colour through shades of grey, brown, and red. A heavy infestation of foot rot was not obtained in any of these plots. The amount of foot rot was least in the plot inoculated with *W. graminis.* As the percentage of diseased plants in the latter plot was practically negligible each season, and many of the plants yielded *F. culmorum* on plating, no attempt was made to assess quantitatively the amounts of disease due to the different organisms in these plots.

(ii) The pathogenicity of different isolates of *W. graminis.*

Of 50 representative isolates tested for their pathogenicity on wheat plants, none showed any significant variation in this respect. The tests were made on plants grown in glass tubes under aseptic conditions, and in pots of sterilized soil.

(iii) Factors which might influence pathogenicity.

Several series of experiments were made to determine whether the pathogenicity of *W. graminis* on wheat plants could be increased by varying the environmental conditions. The percentage of tillers showing brownish superficial discolouration on their bases was slightly increased under certain conditions, but the plants so affected had none of the other typical symptoms of foot rot; i.e. although the susceptibility of plants to attack could be slightly increased, in no case did the organism cause any appreciable ill effect.

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* Mesocotyl = the segment of the seedling axis between the seed and the sheath which encloses the plumular bud (Arber, A., "The Gramineae" (1934), p. 233). Also termed "subcrown internode" or "rhizome" (Percival, J. "The Wheat Plant" (1921), p. 65).

(*a*) *Amount of inoculum.*—A large increase in the amount of inoculum mixed with the soil merely caused a slight increase in the percentage of discoloured stem-bases. Varying amounts of barley-oat grain inoculum up to 200 gm. per 6-inch pot of sterilized soil were used, without producing typical foot rot symptoms, although the general growth, both of plants receiving 200 gm. of inoculum and of controls receiving 200 gm. of sterilized inoculum, was definitely poorer than that of controls receiving no inoculum. This was probably due to the excess of organic matter introduced into the soil. When smaller amounts of inoculum (50 to 70 gm. per pot) were used, they often appeared to have a beneficial effect (see section 7). Amounts below 100 gm. per pot were mixed with the top 2 inches of soil in each pot; amounts of 100 gm. or more were evenly distributed throughout the soil in each pot.

(*b*) *Soil and air temperature and soil moisture.*—Wheat was grown in galvanized iron cans filled with grey sandy loam or red clay loam steamed for 3 hours at atmospheric pressure before use. The cans were kept at moisture contents equivalent to 20, 60, and 85 per cent. of the moisture-holding capacities of the soils, and at average temperatures of 11°, 18°, and 21°C. One-half of the total number of cans were heavily inoculated with *W. graminis* grown on soil-cornmeal mixture,* and the remainder with the same inoculum sterilized just before use.

The plants were examined at maturity, and a disease rating was assigned to those from each can, based on the amount of discolouration of the roots and stem-bases. The disease ratings indicated that the conditions most favorable for attack by *W. graminis* were low to medium temperatures (10° to 15°C.) and medium to high soil moistures (60 per cent. to 85 per cent. of the moisture-holding capacity). The differences between the amounts of discolouration produced under varying conditions were only slight. In no case did the fungus have any detrimental effect on the general growth of the plants.

(*c*) *Soil reaction.*—Two experiments were made to investigate the influence of soil acidity and alkalinity on the pathogenicity of *W. graminis* on wheat. As judged by the frequency of occurrence of discolouration on the roots and stem-bases of the mature plants, attack by *W. graminis* was slightly favoured by soil alkalinity (initial pH of soil from 8.4 to 9.8) and decreased by soil acidity (initial pH of soil from 4.8 to 6.8). There was no sign of disease in the aerial parts of the plants.

(*d*) *Mechanical injury.*—Damaging the seed before sowing (scarifying, puncturing the seed coat over the embryo, or cutting off the brush end), using very shrivelled grain as seed, or cutting back the plants after several weeks' growth, did not affect the liability of the plants to attack by *W. graminis.*

(*e*) *Addition of chemicals to the soil.*—Sodium chloride and zinc nitrate were used at the rates of 0.5, 1.5, and 4 gm. per 6″ pot, and manganous sulphate at the rates of 2, 4, and 8 gm. per 6″ pot. Each of these compounds caused an appreciable reduction in the growth of the plants, but there was no consistent difference in the severity of attack by *W. graminis.*

* One part by volume of cornmeal to 10 of potting soil, moistened and autoclaved for one hour at 15 lb. pressure.

(*f*) *Exposure to arid conditions.*—Wheat was grown in pots of soil inoculated with *W. graminis, F. culmorum,* and *O. graminis.* At or shortly after the flowering stage, the plants were exposed to extremely hot and dry air conditions artificially produced in glass control-chambers for periods ranging from 18 to 48 hours, as were also non-inoculated check plants. They were then allowed to mature under ordinary greenhouse conditions. What appeared to be typical "white-heads" were readily produced in this way, but there was no significant difference between the percentages of white-heads in the inoculated and non-inoculated plants. None appeared on comparable plants not placed in the arid control-chambers.

(*g*) *Conidial inoculation of aerial parts of seedlings.*—The viability of *W. graminis* conidia from a potato saccharose agar culture was first tested by germination in water containing crushed wheat-leaf tissue. Five pots of wheat seedlings 4 to 6 inches high were placed in a moist chamber at 15° to 20° C. for 3 hours, then sprayed with a fresh suspension of spores from the same culture, and replaced in the moist chamber for 48 hours. Controls were similarly treated except that they were sprayed with water only. Guyot (14) reported that a similar experiment made by him resulted in the formation of numerous pycnidia of *W. graminis* near the bases of the inoculated plants between two and three months after inoculation, followed by the death of the plants. In the writer's experiments, no difference could be found between the inoculated and the control lots, both of which made normal growth.

(iv) Joint action of *W. graminis* and other organisms.

(*a*) *Foot rot organisms.*—Sanford and Broadfoot (20) recorded that mixing *W. graminis* inoculum with that of *Ophiobolus graminis* reduced the infection rating of wheat plants from 37.0 (*O. graminis* alone) to 4.8 (*O. graminis* plus *W. graminis*). Under similar conditions, *F. culmorum* and *H. sativum* caused no reduction in the infection rating when mixed with *O. graminis.* In certain of the writer's pot experiments, accidental contamination with *F. culmorum,* presumably due to air-borne conidia from other experiments in the same greenhouse, often occurred in non-inoculated pots or in those receiving sterilized inoculum; it was very seldom found in pots inoculated with *W. graminis.* Subsequent experiments designed to investigate the possibility of biological antagonism between these two fungi showed that *W. graminis* had no influence on the pathogenicity of *F. culmorum.*

(*b*) *Flag smut and bunt.*—Geach (13) showed that infection with flag smut markedly increased the susceptibility of wheat plants to attack by *F. culmorum.* The writer investigated the joint action of *W. graminis* and flag smut (*Urocystis tritici* Koern.) or bunt (*Tilletia tritici* (Bjerk.) Wint.)) on wheat in pot and field experiments during 1934 and 1935. The general procedure used in the pot experiments was that outlined in section 2. In 1934, four treatments were used, viz. (1) 50-70 gm. of barley-oats inoculum of *W. graminis* was added to each 6-in. pot; (2) *W. graminis* was added to the soil as in (1), and the seed was inoculated with flag smut or bunt; (3) as in (1), except that the *W. graminis* inoculum was sterilized by autoclaving just before mixing with the soil; (4) as in (3), but in addition, the seed was inoculated with flag smut or bunt. The four treatments therefore comprised: (1) *W. graminis,* (2) *W. graminis* plus bunt or flag

smut, (3) sterilized *W. graminis* inoculum, (4) sterilized *W. graminis* inoculum plus bunt or flag smut. The methods used for producing bunt or flag smut infection were those described by Angell (1).

The susceptibility of wheat to attack by *W. graminis* was increased only slightly, if at all, by concurrent infection with bunt or flag smut. Sometimes the superficial discolouration of the stem-bases was slightly more pronounced on plants infected with flag smut plus *W. graminis* than on others infected with *W. graminis* only, but in no case was the growth of the plants adversely affected by the latter organism.

In the pot experiments made during 1934, wheat grown in soil mixed with *W. graminis* grown on barley-oats mixture tended to be less severely attacked by flag smut or bunt than wheat on soil mixed with an equal amount of sterilized inoculum. The experiments were repeated in 1935, with the addition of two extra treatments, viz., (1) no inoculum was added to the soil but the seed was inoculated with flag smut or bunt; (2) neither seed nor soil was inoculated.

Three pot experiments and one field experiment were made with flag smut, and two field experiments with bunt. Each of the six treatments in each experiment was replicated ten times in the pot experiments, and eight or nine times in the field experiments. Rod rows were used in two field experiments and half-rod rows in the third. According to the results of these more extensive experiments, *W. graminis* had no significant effect upon the severity of attack by flag smut or bunt. It was therefore concluded that the differential effect noted in the 1934 experiments was due to some undetermined factor, which was perhaps connected with the addition of relatively large quantities of sterile organic matter to the soil in the control pots.

(v) Host range tests.

The organism was isolated from a wide range of artificially inoculated cereals and grasses, although (except possibly in the case of *Hordeum murinum*) it was not found to be any more pathogenic on these than on wheat. Tests were made in pots of sterilized soil and in the field during two seasons. Large amounts of the fungus grown on barley-oats medium were mixed with the soil. The plants were usually allowed to grow until they were nearly mature, isolations from the roots and stem-bases being made before the tops had dried off. Platings were made on acidified potato saccharose agar, the stem-bases being sterilized for 1 to 1½ minutes and roots for ½ to 1 minute in 1:1000 mercuric chloride. A number of inoculations were made with *F. culmorum* and *O. graminis* for comparison.

The results of platings from roots and stem-bases of inoculated plants are given in Table 3. Positive results were much more easily obtained with each of the organisms in pots of sterilized soil than in the field. The field-grown plants inoculated with *O. graminis* often showed abundant black discolouration of the roots, which yielded only saprophytes on plating. This was perhaps due to the difficulty of isolating *O. graminis* from material sterilized in mercuric chloride. Although *W. graminis* could readily be isolated from most of the hosts grown in pots, it appeared to have little or no detrimental effect on them. In some cases, the growth of plants inoculated with this organism was distinctly better than that of those receiving the same amount of

sterilized inoculum or no inoculum. In the pot experiment and in one field experiment, barley grass (*H. murinum*) exhibited a slight stunting and premature ripening, apparently due to attack by *W. graminis*. Sprague (22) found that, in the greenhouse, barley and rye were slightly more susceptible than wheat to the production of superficial lesions by *W. graminis*.

TABLE 3.—RESULTS OF PLATINGS FROM ROOTS AND STEM-BASES OF PLANTS INOCULATED WITH FOOT ROT FUNGI. A + SIGN INDICATES THAT THE ORGANISM WAS ISOLATED; A — SIGN, THAT IT COULD NOT BE ISOLATED; WHERE THERE IS NO ENTRY, NO INOCULATIONS WERE MADE.

Host.	*Wojnowicia graminis.*			*Fusarium culmorum.*		*Ophiobolus graminis.*	
	Sown in Pots, 22.2.33, 20.7.34, &c.	Sown in the Field, 15.4.33.	Sown in the Field (Duntroon), 4.5.33.	Sown in Pots, 1.3.34.	Sown in the Field near Laboratory, 3.5.34.	Sown in Pots, 6.6.34.	Sown in the Field near Laboratory, 26.7.34.
Barley (*Hordeum sativum*, variety Cape)	+		+				
Oats (*Avena sativa*, var. Algerian) ..	+		+				
Rye (*Secale cereale*, var. Black Winter)	+		+				
Maize (*Zea mays*, var. Funk's Yellow Dent)	+	—		+		—	
Feterita (*Sorghum caudatum*) ..	+			+		—	
Perennial rye grass (*Lolium perenne*)	—	—		+	—	+	—
Wimmera rye grass (*Lolium* sp.) ..	—	—		+	—	+	—
Aira caryophyllea ..				+		+	
Avena fatua ..	+	—	—	+	—	+	—
Bromus maximus ..	+	—	—	+	—	—	—
Bromus mollis ..	+	+	—	+	+	+	—
Bromus unioloides ..	+	—	—	+	-	+	—
Danthonia semi-annularis ..		—					
Festuca myuros ..	+		—	+	-	—	—
Hordeum murinum	+	+	—	+	-	+	-
Themeda australis ..	+						

(vi) Varietal susceptibility trials.

Exhaustive tests made with other foot rot organisms by the writer's colleagues gave little or no indication that wheat varieties varied in their susceptibility to attack.* The writer's tests with *W. graminis* were limited to 100 varieties of wheat, Cape barley, Algerian oats, and Black Winter rye. These were grown in 20-foot rows, replicated six times, at Duntroon in 1933, and smaller tests were made in field and greenhouse plots near the laboratory in 1933 and 1934. The only effect produced by *W. graminis* was slight root and stem-base discolouration; no significant variation in the amount of this was found in any of the varieties tested.

* Unpublished data.

6. The Occurrence of Foot Rot Organisms on Apparently Healthy Field-Grown Plants.

The plants attacked by *Wojnowicia graminis* in the writer's pot experiments were usually normal in appearance except for slight discolouration of the basal parts. It was therefore decided to collect a number of apparently healthy plants from field plots on soil infested with *W. graminis,* to determine whether the organism could be isolated from them. The results are summarized in Table 4. Collections were made at five stages of growth, from a plot of about 1 acre of

TABLE 4.—PERCENTAGES OF HEALTHY AND DISEASED WHEAT PLANTS FROM WHICH *Wojnowicia graminis* WAS ISOLATED AT VARIOUS STAGES OF GROWTH.

Date.	Average Height of Plants.	Stage of Growth.	Healthy Plants.		Diseased Plants.	
			Number Plated.	Percentage from which *Wojnowicia graminis* was Isolated.	Number Plated.	Percentage from which *Wojnowicia graminis* was Isolated.
June 18	4 inches	Low, spreading growth ..	50	0	10	0
Oct. 4	1 foot ..	Approaching earing ..	64	16	31	6
Oct. 23	18 inches	Flowering	40	27	..	..
Nov. 20	3 feet ..	Grain in hard dough stage	40	37	..	..
Jan. 3	3 feet ..	Just ready to harvest ..	128	40	181	35

Florence wheat, growing on land which was infested with *W. graminis* and used for a varietal resistance trial the previous year. No inoculum was applied in the year the collections were made. The plants designated "healthy" in Table 4 were of normal size and appearance, with well-filled ears, and were taken from positions at regular intervals throughout the plot; those termed "diseased" showed signs of foot rot, viz., marked stunting, premature withering, or white-heads. In selecting healthy plants, no notice was taken of basal discolouration, provided the plants were otherwise normal. From each plant collected, the base of one culm was plated on acidified potato dextrose agar, after sterilization for 1½ minutes in 1:1,000 mercuric chloride. According to the data in Table 4, *W. graminis* was isolated more often from "healthy" than from diseased plants. The percentage of healthy plants from which *W. graminis* was isolated increased as the crop approached maturity. Healthy mature plants were also taken from three other plots, which had been inoculated with *Fusarium culmorum, Helminthosporium sativum,* and *Ophiobolus graminis,* respectively, at some time previous to that season. Of a total of 51 mature plants from these plots, 17 yielded *F. culmorum,* 2 *W. graminis,* and 1 *H. sativum.* These results show that the occurrence of W. *graminis* in association with foot-rotted plants is inadmissible as evidence that this organism is the cause of their diseased condition, since it occurs also on plants grown under similar conditions but showing no signs of foot rot.

7. The Effect of *Wojnowicia graminis* on the Yield of Wheat.

The results of inoculations in pots showed that *W. graminis* was very weakly, if at all, pathogenic on wheat. The experiments described below were planned to determine whether the organism had an effect on yield too slight to be evident in the preliminary qualitative pathogenicity tests. Large quantities of inoculum were used in most of the experiments. This involved the addition of much organic matter to the soil, which in itself might be expected appreciably to influence the yield. This disturbing factor was admitted in the hope of obtaining the maximum practicable infestation.

The effect of *W. graminis* on the yield* of wheat was investigated in three pot and three field experiments during 1935. These were combined with the experiments on the joint action of *W. graminis* and flag smut or bunt, already mentioned in section 5. Only those portions of the experiments concerned with the effect of *W. graminis* and of sterilized inoculum on yield, as compared with the yield of normal untreated plants, will be dealt with here.

The results of the three pot experiments are summarized in Table 5. In each experiment, 10 six-inch pots of a mixture of loam, sand, and compost were used for each treatment. The soil was steamed for three hours at atmospheric pressure, and the inoculum was added

TABLE 5.—RESULTS OF POT EXPERIMENTS ON THE EFFECTS OF *Wojnowicia graminis* AND OF STERILIZED INOCULUM ON THE YIELD OF WHEAT, AS MEASURED BY AIR-DRY WEIGHT OF MATURE AERIAL GROWTH.

Experiment.	Average Air-dry Weights of Aerial Growth in Grams per Pot (Five Plants).			Standard Error of Mean Dry Weight per Pot for each of Treatments I., II., and III.	Significance of Differences between Average Yields for each Treatment.
	I. *W. graminis.*	II. Sterilized Inoculum.	III. No Inoculum.		
A	11·2	12·1	10·7	0·53	No significant differences
B	12·72	11·31	8·58	0·44	Differences between each pair of yields are significant
C	10·54	8·36	6·82	0·82	Yield from I. significantly higher than yield from III.
Combination of three experiments	11·55	10·75	8·84	0·41	Yields from I. and II. significantly higher than yield from III.

within a day after steaming. In Experiments A and B (see Table 5) series I received 50 gm. of inoculum (*W. graminis* on oats-barley mixture) per pot; series II. received the same sterilized just before addition to the soil; series III. was untreated. In experiment C, no grain inoculum was used. Instead, the organism was grown on oatmeal agar, on which numerous pycnidia were formed, and the cultures

* In the pot experiments, "yield" refers to total dry weight of mature aerial parts; in the field experiments, it refers to weight of grain.

were macerated with water to form a suspension of conidia and hyphal fragments, from which the agar was removed by filtering through cheesecloth. Each of the pots in series I. received an equal volume of this suspension, and each in series II. received the same volume of sterilized suspension. Series III. was untreated. In the three experiments 10 seeds of Canberra wheat per pot were sown at the time the inoculum was added to the soil. The resultant growth was thinned to five plants per pot about a month later. The pots were kept out of doors for most of the growing period. Shortly after the plants matured, the aerial parts were cut off at ground level, air-dried, and the produce of each pot weighed separately; the yield of grain was not determined. The results were subjected to analyses of variance (5). As will be seen from Table 5, no significant differences between treatments were revealed by experiment A. In experiment B, the *W. graminis* series gave a significantly higher average yield than did the sterilized inoculum series, and the latter gave a significantly higher yield than the untreated series. In experiment C, the *W. graminis* series gave a significantly higher yield than the untreated series, the sterilized inoculum series giving an intermediate yield not significantly different from either of the other two yields. On subjecting the combined results of the three experiments to a further analysis of variance, the yield from the untreated series was found to be significantly lower than those from either of the treated ones. There was no significant difference between the latter two yields, indicating that the increase of yield in both these series was probably due merely to the manurial effect of the inoculum.

The results of the three field experiments are summarized in Table 6. The experiments were laid out on the randomized block system as described by Fisher and Wishart (5) and the results were examined statistically according to the method given in that publication. In experiment A, there were nine replications of each treatment; in experiments B and C there were eight. Experiments A and B were conducted on a silty loam of medium texture near the laboratory; A was on an area on which wheat inoculated with *W. graminis* was grown during the previous two seasons; and B was on grass land ploughed for the first time a few weeks before seeding. Experiment C was on a heavier reddish clay loam at Duntroon, cropped at least once before, though not previously artificially infested with *W. graminis*; the organism occurs naturally in similar land nearby. In each experiment, soil inoculum prepared as described in section 2 was applied at the rate of 1 kgm. per 8 ft. 3 in. of row to series I., the same sterilized by autoclaving just before use to series II., and series III. was untreated. Every experimental row was between two untreated guard rows, the distance between rows being 1 foot. Superphosphate was applied to each row at seeding time, at a rate equivalent to about 1 cwt. per acre.

For unknown reasons, the germination was very unsatisfactory in experiments A and C; in A, series I. (*W. graminis*) gave much the best germination, as shown in Table 6. The uneven germination resulted in very variable numbers of plants maturing per row. Practically every seed which germinated produced a mature plant. In Table 6, the yields are presented in two ways: (1) the average yield of grain per row; (2) a figure obtained by dividing the yield for each row by the number of plants in that row, multiplying by 100, and averaging the eight or nine

TABLE 6.—RESULTS OF FIELD EXPERIMENTS ON THE EFFECT OF *Wojnowicia graminis* AND OF STERILIZED INOCULUM ON THE YIELD OF WHEAT.

Experiment.	Variety of Wheat.	Number of Replications.	Length of Row.	Kilograms of Soil Inoculum per Row.	Number of Seeds Sown per Row.	I. *Wojnowicia graminis*.			II. Sterilized Inoculum.			III. No Inoculum.			Standard Error of Mean Yield per Row for each Treatment.	Significance of Differences between Average Yields for each Treatment.*
						Average Number of Plants Harvested per Row.	Average Yield of Grain in Grams.		Average Number of Plants Harvested per Row.	Average Yield of Grain in Grams.		Average Number of Plants Harvested per Row.	Average Yield of Grain in Grams.			
							Per Row.	Per 100 Plants.		Per Row.	Per 100 Plants.		Per Row.	Per 100 Plants.		
A	Aussie ..	9	8′ 3″	1	50	42	184·0	443	23	100·7	439	32	120·6	378	10·6	Yield from I. significantly higher than yields from II. or III.
B	Aussie ..	8	16′ 6″	2	100	98	347·3	356	96	341·5	353	96	278·7	289	14·4	Yields from I. and II. significantly higher than yield from III.
C	Ford ..	8	16′ 6″	2	100	64	444·6	723	66	421·8	711	51	343·9	724	16·4	Yields from I. and II. significantly higher than yield from III.
A + B + C	..	..	..	..	..	..	385·9	505	..	316·8	499	..	285·7	460	10·4	Differences between each pair of yields are significant

* " Yield " in this column means average yield of grain per row.

corrected yields thus obtained for each series in each experiment. The first figure represents the combined results of the effects of the treatment upon plant establishment and yield per plant; the second represents the effect of the treatment upon yield per plant; in both cases the effect on yield is more or less obscured by the effect of uneven spacing. Analyses of variance of yield of grain per row were made for each experiment and for the combined results of the three experiments. In the latter case, the yields per row in experiment A were doubled in order to make them directly comparable with those in experiments B and C.

In experiment A, the average yield both per row and per 100 plants was highest in series I. (*W. graminis*), although in series II. each plant had on an average almost double the space in which to grow; in the other two experiments, series I. gave the highest mean yield per row, but the difference between this yield and that of the next highest (series II. —sterilized inoculum) was not statistically significant. In experiments B and C, the yields from the untreated rows were significantly less than those from either series of treated rows, which seems to indicate that the inoculum had a manurial effect, apart from the presence of living *W. graminis*. The analysis of variance of the combined results of the three experiments showed that the yield from series I. was significantly higher than that from series II., and the latter was significantly higher than the yield from series III. Although the difference between the average yields from series I. and II. is largely accounted for by the small number of plants harvested in series II., experiment A, the results from pot and field experiments considered as a whole give some grounds for the belief that, under certain conditions, the presence of *W. graminis* inoculum may have a stimulating effect on the germination and yield of wheat. It cannot be assumed, however, that *W. graminis* is directly responsible for this beneficial effect, until the foregoing evidence is confirmed by experiments in which complicating factors, such as uneven plant establishment and manurial or toxic effects of inoculum, are reduced to a negligible minimum. It is possible, for instance, that the failure of sterilized inoculum to cause as high a yield as unsterilized inoculum may be due to some injurious effect of the former, to stimulation of the plants by *W. graminis,* or to a combination of both effects. There is certainly no evidence that *W. graminis* is detrimental to the growth of wheat.

8. Conclusions.

The data here presented support the opinion held by most previous workers, that *W. graminis* is only very slightly, if at all, pathogenic on wheat, and of little or no importance in this connexion, despite its wide distribution and frequent association with foot-rotted plants. There remains the possibility that it may parasitize wheat more strongly under conditions at present unknown.

No experiment has revealed any depression of the yield of wheat due to inoculation with *W. graminis*. There is some evidence that the organism may adversely affect the growth of other plants, e.g., barley grass; under certain conditions it appears to produce more marked lesions upon barley and rye than on wheat (22), but there is no evidence that it decreases the yield of these crops.

The increase produced in the yield of wheat in some of the writer's experiments by *W. graminis* inoculum, and to a lesser extent by sterilized inoculum, cannot be satisfactorily explained from the data at present available. These results illustrate the necessity, already demonstrated by other workers, of taking into consideration the possibility that the addition of inoculum to the soil may seriously affect the growth of plants in ways not directly due to the living organism contained in the inoculum. Hynes (25) found that certain weakly parasitic strains of *Helminthosporium sativum, H. tetramera,* and *Ophiobolus graminis* appeared to stimulate the growth of inoculated plants. The growth of rice seedlings was found by various workers to be stimulated by *Gibberella fujikuroi;* Edwards (24) observed that *G. fujikuroi* var. *subglutinans* caused the premature germination of infected maize grain. Possibly, the growth of wheat sown in soil infested with *W. graminis* may be stimulated by this organism in a similar way.

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61. Studies in the Supplementary Feeding of Merino Sheep for Wool Production.—I.
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67. Methods for the Identification of Coloured Woods of the Genus Eucalyptus
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